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LABORATORY METHODS FOR MAINTAINING AND STUDYING WEB-BUILDING SPIDERS

Samuel Zschokke: Department of Integrative Biology, Section of Conservation Biology (NLU), University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland. E-mail: samuel.zschokke@alumni.ethz.ch

Marie E. Herberstein: Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

ABSTRACT. Web-building spiders are an important model system to address questions in a variety of biological fields. They are attractive because of their intriguing biology and because they can be fairly easily collected and maintained in the laboratory. However, the only published instructions for working with web-building spiders are somewhat outdated and not easily accessible. This paper aims to provide an up-to-date guide on how to best collect, keep and study web-building spiders. In particular, it describes how to obtain spiders by capturing them or by raising them from cocoons, how to keep and feed spiders in the laboratory and how to encourage them to build webs. Finally it describes how to document and analyze web building and web structure.

Keywords: Data collection, laboratory manual, methodology, spider silk, spider web

Web-building spiders are a popular model system to address questions in various scientific fields such as physiology, ecology, evolutionary biology, ethology and chemistry. Silk production, while not unique to this group, is its most characteristic feature (Craig 1997). Physiologists aim to understand how silk is produced while chemists investigate its properties and structure (e.g., Vollrath 1999; Knight & Vollrath 2001). Webs built out of silk are used to catch insects, making web-building spiders important predators, and even biological control agents (e.g., Riechert 1999; Symondson et al. 2002). As prey remains are often retained in the web post-consumption, prey capture can easily be assessed. The evolution of the web in itself has been studied extensively (e.g., Eberhard 1982; Coddington & Levi 1991; Benjamin & Zschokke 2004). Similarly, sexual cannibalism, prevalent in several families of web-building spiders, or sperm competition and cryptic female choice have been the focus of many exciting studies (see Elgar 1998; Eberhard 2004 for reviews).

Web-building spiders are also attractive to scientists because they can be easily collected and maintained in the laboratory, allowing large sample sizes and large-scale experiments. However, many researchers who recognize the value of spiders as model systems may be inexperienced in collecting and maintaining web-building spiders. With the present paper we aim to provide the necessary information, in the hope to foster cross-disciplinary studies on these fascinating creatures.

With towards 40,000 described spider species (Platnick 2005), we cannot give specific information for each species. Such information can be obtained either when collecting the spiders in their natural habitat or from researchers experienced with that spider species. Here we focus on species we have worked with, i.e. mainly orb-web spiders, but attempt to make our recommendations applicable to all web-building spiders, especially since much research is still needed on webs of most non orb-web spiders.

OBTAINING SPIDERS

We recommend obtaining spiders by collecting them in the wild, thereby gaining a first impression of web structure and physical requirements. As most web-building spiders build webs only under favorable weather conditions, they are best found when it is neither raining nor very windy. We do not recommend obtaining spiders from dealers, since the source of these spiders is often unclear and they may be inbred.

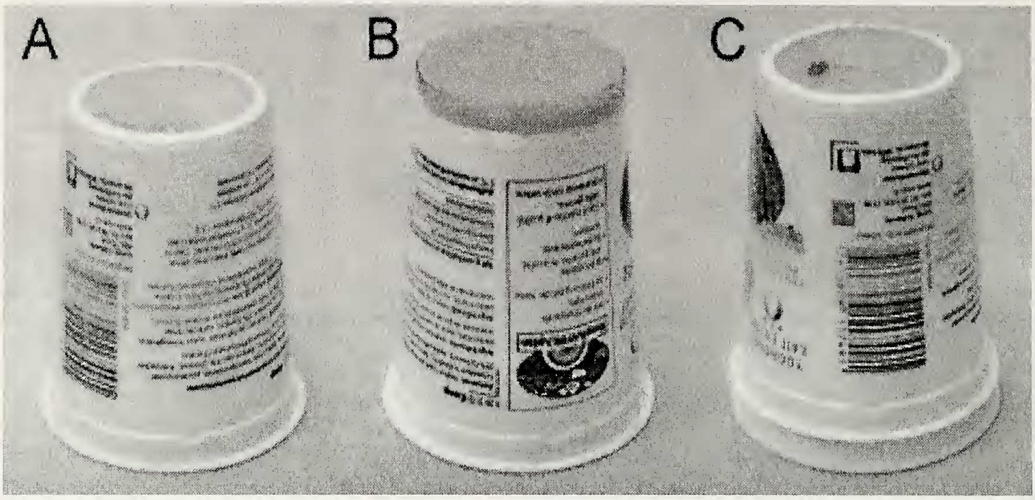

Figure 1.—"Spi-pot", a simple device to temporarily immobilize a spider for identifying or measuring (modified after Roberts 1995). It consists of two equally sized, round plastic pots. In one pot (pot A), a round hole is cut into its base, leaving a rim of c. 5 mm for rigidity. This hole is then covered with tightly stretched cling wrap, secured along the sides with tape. On the base of the other pot (pot B) a circular piece of soft foam is glued. The thickness of the foam should correspond to the gap at the base when two pots are stacked inside each other. To examine or measure a spider, place it in pot A, push pot B inside pot A and view the spider through the cling film (C).

Capturing spiders.—To capture an orb-web spider sitting in its web, place a small jar around the spider and replace the cover from the other side of the web. If the web should remain undamaged for photos, tap the web opposite the spider, causing the spider to drop down into a container held below. To capture a spider hiding in a retreat, either collect the entire retreat or lure the spider out of the retreat by placing a vibrating tuning fork on the web (if no tuning fork is at hand, vibrating forceps sometimes also work; Penney 1995). Theridiid and linyphiid spiders may require a larger jar, lifted up quickly from below around the spider in its web. Do not use butterfly nets to capture web-building spiders as this can damage them.

Immature or sub-adults females will have a longer life expectancy than adults and seem to thrive better in the laboratory, whereas adult males do not build webs and adult females may soon start laying eggs, and then build less regular webs. For studying mating behavior, it is essential to control the spiders' mating histories. Unfortunately, identifying sub-adult, live spiders in the field can be difficult or impossible. A good aid to examine live spiders is the "Spi-pot" (Roberts 1995; Fig. 1). For transport, spiders can be housed in film canisters of 35 mm or APS films. Using the semi-transparent variety, allows checking the spider without opening the canister. Leaves or twigs give the spider a substrate to hang onto and provide some humidity. Place spiders singly in containers to prevent cannibalism.

Sending live spiders.—To send spiders by courier or ordinary airmail, put them into a fairly airtight container with a small piece of moist cotton or paper towel to prevent desiccation. The air enclosed in the container is sufficient for many days, and feeding is not necessary during shipment.

Legal aspects.—In certain areas or countries, capturing some or all spider species is not allowed or requires permits from the relevant authorities. Similarly, import and export permits and restrictions must be observed when sending or transporting spiders between countries.

Rearing spiders from eggsacs.—The easiest starting point to rear spiders from eggsacs are gravid, mated females collected in the field. It is virtually impossible to know whether a female has mated, but the likelihood of collecting a mated female increases with the progression of the season. Unmated females will also eventually lay eggs, albeit infertile ones. When the spider has built a cocoon, it must be exposed to appropriate climatic conditions, similar to those in its natural habitat. We found it helpful to keep cocoons of various web-building spiders in a chicken egg incubator made of Styrofoam and with a rough temperature control and a water reservoir to maintain humidity levels to prevent desiccation of the cocoons. Unfortunately, eggs often fail to hatch, and even if they do, rearing the spiderlings is a real challenge (see below).

HUSBANDRY OF SPIDERS

Enclosures (frames) to keep spiders.—A variety of frames have been used to study spiders and their webs. In the laboratory of Peter Witt, elaborate metal cages were used (Witt 1971). We suggest simpler frames entirely made out of Perspex. The frame's size should correspond to the web size; initial field measurements may therefore be necessary. To house small to medium sized orb-web spiders (e.g., *Zilla diodia* (Walckenaer 1802), juvenile *Araneus diadematus* Clerck 1757 or *Larinioides sclopetarius* (Clerck 1757)), we used frames consisting of four pieces of transparent Perspex, 5 cm wide, 30 cm long and 3 mm thick, glued together with industrial strength glue at the corners (Fig. 2). Large orb-web spiders (e.g., adult *Argiope* sp.) require frames made out of 50 cm long Perspex pieces and adult *Nephila* sp. require even larger frames. Similar frames, but laid horizontally, can be used for sheet-web spiders (Bartels 1929). Spiders building three-dimensional webs (e.g., linyphiid and theridiid spiders) require cube-shaped frames. For some species it can be advantageous to build the frames higher than wide. To facilitate the spider's grip to the frame's inside, apply net-like crack-seal tape, painted black beforehand to reduce unwanted reflections when later taking pictures of the web. To allow unobstructed examination of the web, the spiders must be kept in frames where two opposite sides can be removed.

To separate the frames, place thin (0.5 mm), large (a few cm larger than the frames), transparent and somewhat flexible PVC sheets between them. These sheets are smeared with Vaseline to deter spiders from attaching threads. Alternatively, windowpanes, which are kept very clean, can be used. In addition, puffy foam can be put along the edge of the frame, encouraging spiders to attach to that foam rather than to the glass. The frames are put on a shelve like books with the thin sheets placed between them (Fig. 3). When a spider has built a web, its frame can be easily taken from the shelf and placed in front of a shadow box for examination (see below, taking pictures). When handling the frame carefully, the spider usually stays in its web (or retreat). Some freshly caught spiders are likely to leap off the web or leave the hub of the web when their frame is handled for the first time, but will mostly become habituated to being handled after a few days.

There are many alternatives to the durable Perspex frames described above, which may suit short-term or preliminary experiments, such as using rigid cardboard, wooden frames or 'slices' of round plastic buckets with cling wrap to prevent spiders from escaping. Spiders building webs on rather than between supports can be offered an artificial, standardized structure to build their web on (Blackledge & Wenzel 2001), which is then placed inside a larger container with clean, smooth sides.

For short-term storage of smaller spiders we use upturned plastic cups from which the bottom has been removed and replaced with a fine mesh. Smaller spiders will build small webs in these cups, which can be misted from the top (with a spray bottle) without lifting the cup. Alternatively, only a small hole is cut into the bottom of the cup and corked with a cotton plug or a tampon piece. Water is then administered by wetting the cotton plug. Keeping spiders in such small cups can also be an experimental procedure; e.g., when studying web-building behavior, larger spiders can be maintained in cups to temporarily prevent them from building webs (e.g., Reed et al. 1970; Herberstein et al. 2000).

Feeding and watering.—Spiders can be fed with almost all kinds of insects, and most web-building spiders will attack and overwhelm insects trapped in their web in a large range of sizes, up to their own size or even larger. *Drosophila* flies are often used, as they are easily reared. When rearing *Drosophila* in bottles with sponge stoppers, spiders can be fed by trapping single flies between the flange of the stopper and the bottle, from where they can be introduced into the web using forceps. Spiders without webs are trickier to feed; some spiders accept live prey held near their mouth with forceps; buzzing flies are more

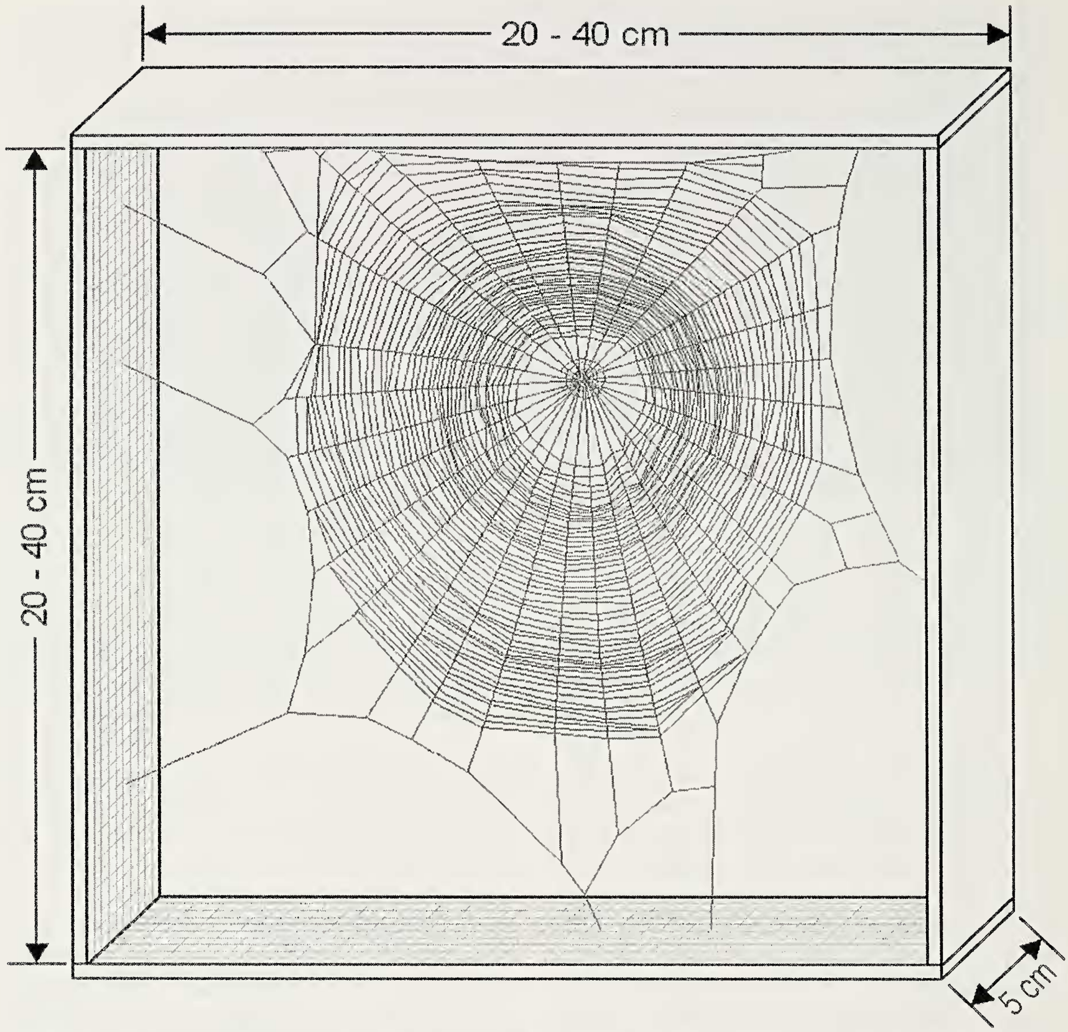

Figure 2.—Frame to keep orb-web spiders made out of four Perspex strips, glued together at the corners (not to scale). On the inside of the frame, blackened crack-seal tape has been applied to facilitate the spider's grip. Similar frames with dimensions accordingly adapted can be used for other web-building spiders.

readily accepted than kicking crickets. Sprinkling water over the offered insect or breaking the insect's cuticle a bit by snipping a cercus or antenna to release a drop of hemolymph can induce spiders to feed when the liquid touches the spider's chelicerae. It is sufficient for most spiders to be fed once per week. However, since feeding spiders without web can be tricky, we recommend feeding spiders twice per week. Feed spiders at least so much that they do not loose substantial amounts of weight, causing their abdomens to shrink. Whereas some spiders can be kept for a prolonged time on such a minimal diet (in our experience e.g., *Araneus diadematus*, *Zygiella x-notata* (Clerck 1757)), other species seem to falter when they are not given enough food to grow (e.g., *Argiope bruennichi* (Scopoli 1772)). Natural prey capture rates may provide helpful starting points when designing feeding regimes in the laboratory. It is important to either feed the spiders with different insects or to feed the prey insects with high quality food (i.e. supplemented with proteins, vitamin-enriched cereal or pet food), as the spiders may otherwise experience deficiencies (Uetz et al. 1992; Mayntz & Toft 2001). The relatively dry air in most buildings makes spi-

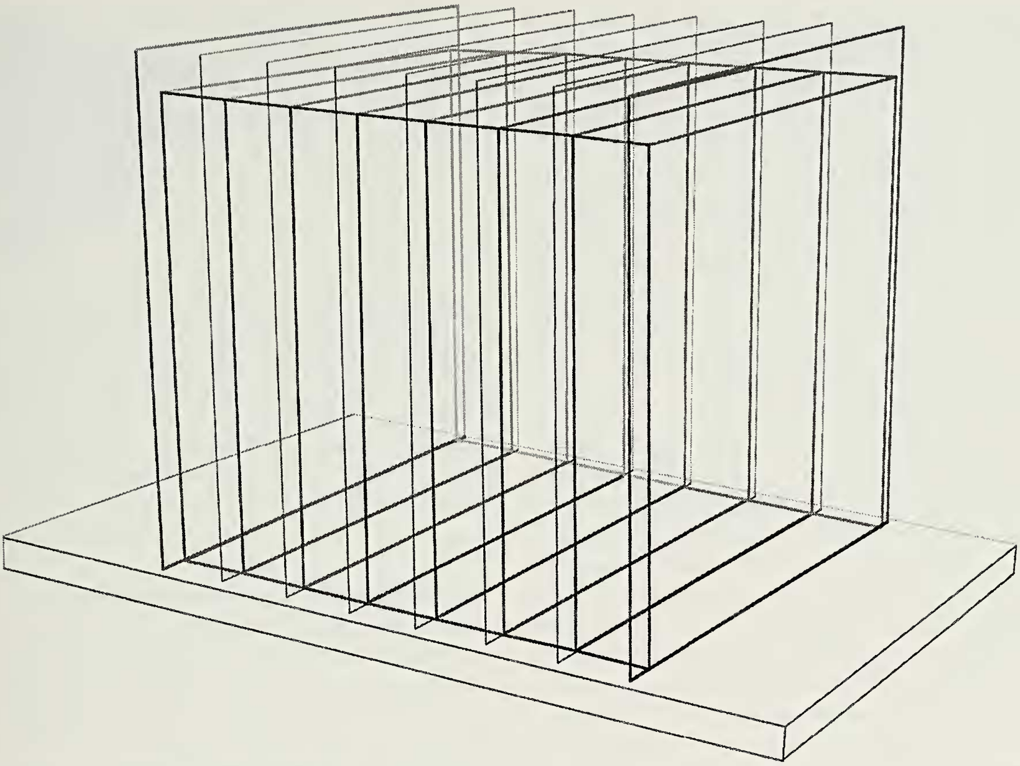

Figure 3.—Several frames (cf. Fig. 2) put side to side on a shelf. Thin PVC sheets placed between adjacent frames prevent the spiders from moving between frames. The thin sheets are smeared with Vaseline to prevent the spiders from attaching threads. The first and the last sheet are thicker, more stable ones, held up with bookends (not shown).

ders kept inside vulnerable to desiccation. Thus regular misting with a water sprayer or placing a moist sponge at the bottom of the frame is vital. For experiments on the impact of drugs or pesticides on web building consult earlier studies on how to administer drugs (e.g., Witt et al. 1968; Witt 1971; Samu & Vollrath 1992; Hesselberg & Vollrath 2004).

Rearing spiderlings.—This is notoriously difficult and fraught with high levels of mortality. To rear spiderlings, place the freshly hatched cocoon into a container with support for the webs such as wood-wool, and add cultures of *Drosophila* or Collembola as food (Dinter 2004). Initially, some spiderlings will consume each other; more established ones then construct webs and capture prey. Do not separate the spiderlings too early as this can lead to almost total mortality.

Encouraging web building.—Spiders vary greatly in their propensity to build a web in the laboratory. It is possible to find out which spider species build webs readily by identifying species used in earlier laboratory studies. The most popular orb-web species include *Araneus* sp., *Argiope* sp., *Nephila* sp. and uloborid spiders. In contrast, *Gasteracantha* sp., *Tetragnatha* sp., *Meta* sp., *Metellina* sp. and *Leucauge* sp. are more hesitant to build webs. Feeding a spider that has not yet built a web in the laboratory, or putting a live fly into the cage together with the spider (Pasquet et al. 1994) can help to induce web building. If releasing a live fly into the frame with the spider is problematic because of strict feeding regimes, flies can be kept in a small jar with some sugar solution and covered by fly mesh. This way the flies buzz and stimulate web building without being captured by the spider (Herberstein et al. 2000). Web building frequency is also higher when spiders are exposed to natural day—night cycles in light and temperature (Witt 1956).

Once the spider has built its first web in the laboratory, feed it soon to encourage the spider to build again. Web building frequency varies between species. Whereas *Araneus diadematus*, *Argiope* sp., *Larinioides sclopetarius* and *Zygiella x-notata* generally rebuild the capture area of their web every night or every other night, *Nephila* sp. typically rebuild only sections of the web.

Damaging webs.—Some orb-web spiders hesitate to rebuild their web as long as it is intact. To induce web rebuilding, it may therefore be necessary to damage or destroy the webs. In the field, spiders generally leave the frame and the anchor threads largely intact when rebuilding the web (Carico 1986). Thus, only the capture area should be damaged to induce rebuilding, e.g., by cutting holes into the capture area with a red-hot wire (Fig. 4). Alternatively, cut the lateral anchor threads with scissors to destroy the entire orb-web. However, complete web destruction forces the spider to build the next one from scratch, which can influence aspects of the web (Zschokke & Vollrath 2000). In general, the spider should be allowed to ingest the old web (Peakall 1971). Damaging a single sticky spiral segment allows to determine whether the spider rebuilds the web during the next night.

Non orb-web spiders do not remove, ingest and rebuild their web as orb-web spiders do, but keep repairing and extending them (Tanaka 1989; Benjamin & Zschokke 2003, 2004). To study the construction of these webs, remove the old web completely or place the spider in a new frame.

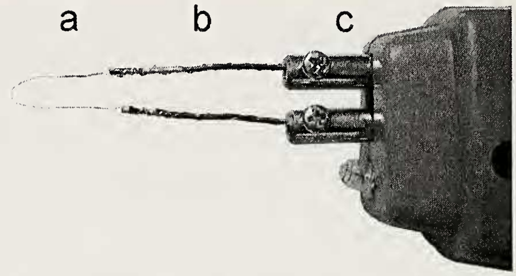

Figure 4.—Tip of a modified soldering gun used to selectively damage parts of a web. The thick wires (b) emerging from the front of the soldering gun (c) are either parts of the original tip or wires as found in 220 V wires. Soldered to these thick wires is a single strand of a 220 V cable (a). To ensure good contact between wire and strand, the strand is wrapped around the wire.

DATA COLLECTION

Observing web building.—Observing spiders during web building is not easy because they are very sensitive to disturbance, especially during the early stages of web building (which are therefore least well known; Zschokke 1996) and because the time of web building is generally during the night but otherwise largely unpredictable, likely depending on changes in temperature or light (Spronk 1935; Witt 1956). Observing web building is additionally impeded by the light sensitivity of most web-building spiders. Again, spiders differ in their sensitivity. *Araneus diadematus*, *Nephila plumipes* C.L. Koch 1839 and *Argiope keyserlingi* Karsch 1878 are fairly tolerant to some light and may even rebuild their web during the day, whereas other species (e.g., *Nuctenea umbratica* (Clerck 1757), *Zygiella x-notata*) will only build in absolute darkness. These difficulties can be overcome by using automated spider tracking under infrared light (Benjamin & Zschokke 2002). This method additionally records the spider's time budget, but neither records the position of threads nor all details of the spider's behavior.

Taking pictures.—Since spider web silk is very thin (c. 0.5 μm–5 μm), taking pictures of spider webs with all threads clearly visible is difficult. Earlier studies suggested placing the entire web in a box filled with ammonium chloride (Peters et al. 1950) or coating it with white glossy spray paint (Witt & Reed 1965) to increase thread visibility. However, these approaches require removing the spider from the web, they may distort the web and prevent spiders from ingesting the web, as orb-web spiders usually do (Peakall 1971), or to keep using it as non orb-web spiders do. Good pictures of spider webs can also be obtained with untreated webs. The main requirements are bright light from the sides and a very dark background, such as a shadow box lined with black velvet (Langer & Eberhard 1969; Zschokke 2002). We obtained satisfactory results using two 15W fluorescent bulbs on either side of the web with an aperture of 4.5 and an exposure of 1 sec. when using a 55 mm lens on a SLR camera loaded with 100 ISO B/W film (Agfapan). To further improve picture quality, add two bulbs along the top and the bottom of the web. When using a digital camera, a good resolution (at least 3–4 Megapixels) is essential. Since the picture is mostly dark, with fine white lines, use manual settings, as the automatic settings of most cameras will produce inferior to unusable results. Every photograph should be recorded in a lab book and, to avoid any possible confusion, include a marker along the edge of the picture for identification, together with a scale and an indicator for the top of the web.

Describing webs.—Several approaches have been proposed to estimate the area of orb-webs (Herberstein & Tso 2000 for *Argiope* sp. webs and Blackledge & Gillespie 2002 for webs of *Cyclosa* sp. and *Tetragnatha* sp.), as well as the total thread length as a measure of the spider's investment (Heiling et al. 1998 for *Larinoides sclopetarius* webs and Venner et al. 2001 for *Zygiella x-notata* webs). These approaches require measurements of various web parameters, including number of spiral turns, and capture and hub area dimensions. Their suitability depends on the web shape, and whether field or laboratory measurements are made. Field measurements are difficult and it may be wise to select a formula requiring only few measurements; a reduced measuring accuracy can be compensated with a larger sample size (Zschokke & Lüdin 2001). Even though measurements in the laboratory are easier and more precise, these formulae only provide estimates. To obtain accurate data, take a photograph of the web (see above) and import it into a graphics program that calculates area or thread length digitally.

In the past, a multitude of names have been used for the various parts of webs. To avoid confusion, use established names (Zschokke 1999 for orb-webs). Similarly, with names of some spider species changing over the years, make sure to use the current species name (Platnick 2005).

Measuring spiders.—Spider size refers to the length or width of a sclerotized body part, such as leg length (typically the tibia-patella length of the first leg is used) or carapace width. As these parts do not grow between molts, they provide information on the growth rate prior to the previous molt; and they can be relevant web parameters (e.g., leg length can influence mesh size in orb-webs; Vollrath 1987). Live spiders need to be immobilized for measuring with a Spi-pot (see above) or with CO_2. When using CO_2, gently blow CO_2 into a sealable jar with the spider until the spider stops moving; taking care not to kill the spiders with too much CO_2. Large spiders can be measured with electronic calipers, small ones under a dissecting microscope with an ocular fitted with a reticule. Keeping the exuviae of the spiders allows later size measurements. Spider weight is also an informative and fairly easily obtained measure. Weight in addition to size can then be used to estimate recent foraging success by calculating spider condition (weight / size or residuals of weight / size; Jakob et al. 1996; Kotiaho 1999).

CONCLUSIONS

Web-building spiders provide excellent models to test general and spider-specific hypotheses. Collection and maintenance of juvenile and adult spiders is relatively easy, ensuring large sample size and power. While rearing juveniles from eggs is difficult, some research groups have achieved relatively high rates of survival. Manipulation and observation of web-building spiders in the laboratory is simple and can be achieved by non-arachnologists by following some basic rules set out above.

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